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HYBRIDS IN AMERICAN CYATHEACEAE

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Several small tree ferns collected in a ravine near Cerro de Punta, Puerto Rico, are proposed as a hybrid between *Alsophila dryopteroides* (Maxon) Tryon and *Nephelea portoricensis* (Kuhn) Tryon, both of which were growing abundantly at the site. This is the first unequivocal report of a hybrid in the family.

In addition, six other hybrids are proposed, one on the basis of substantial evidence, and the others on the basis of inference. Four previous reports suggest that hybridization may occur in the Cyatheaceae, but definitive analyses of the parental and hybrid characters were not presented. Holttum and Sen (1961) and Holttum (1963, 1974) report that *Cyathea alternans* (Wall ex Hook.) Presl of Malaya, Sumatra and Borneo might be a series of hybrids between *Cyathea moluccana* R. Br. and *C. squamulata* (Bl.) Copel. on the basis of its indusium and leaf architecture. Gastony (1973) treats *Nephelea concinna* (Kuhn) Tryon as a species but notes the possibility that it is a hybrid between *N. pubescens* (Kuhn) Tryon and *N. Tussacii* (Desv.) Tryon on the basis of intermediate characters of the lamina architecture and partially contracted fertile pinnules.

DEFINITE HYBRIDS

1. **Alsophila dryopteroides** (Maxon) Tryon × **Nephelea portoricensis** (Kuhn) Tryon

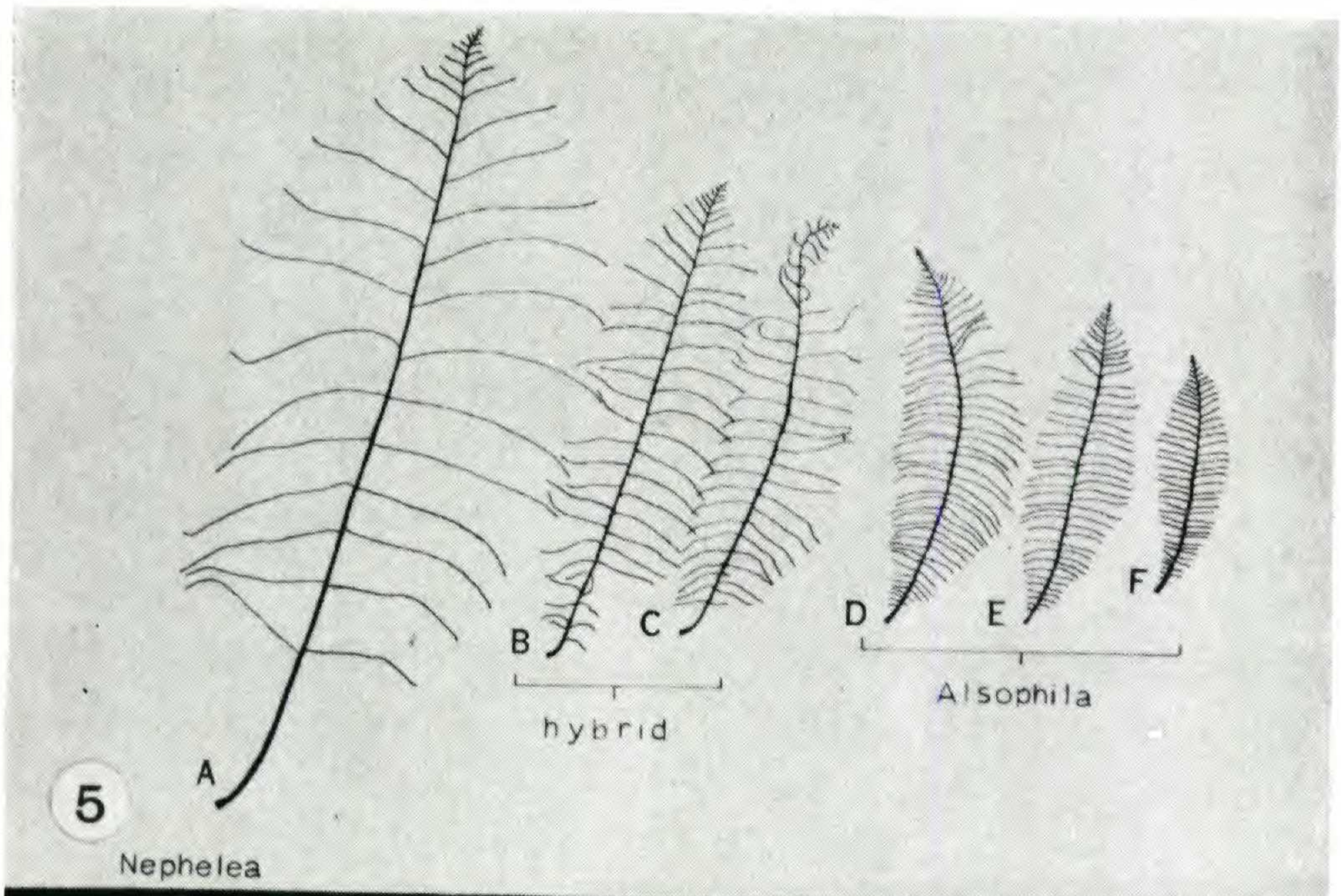
Plants of this hybrid (Fig. 1) resembled large plants of *Alsophila dryopteroides* at a distance, but on closer inspection they were seen to have the black squaminate spines of *Nephelea* on the petiole. Species of Cyatheaceae growing nearby were *Lophosoria quadripinnata* (Gmel.) C. Chr., *Cyathea arborea* (L.) Sm., *C. furfuracea* Baker, *Trichipteris armata* (Sw.) Tryon, *T. borinquena* (Maxon) Tryon, *Alsophila bryophila* Tryon, *A. dryopteroides* (Maxon) Tryon, and *Nephelea portoricensis* (Kuhn) Tryon.

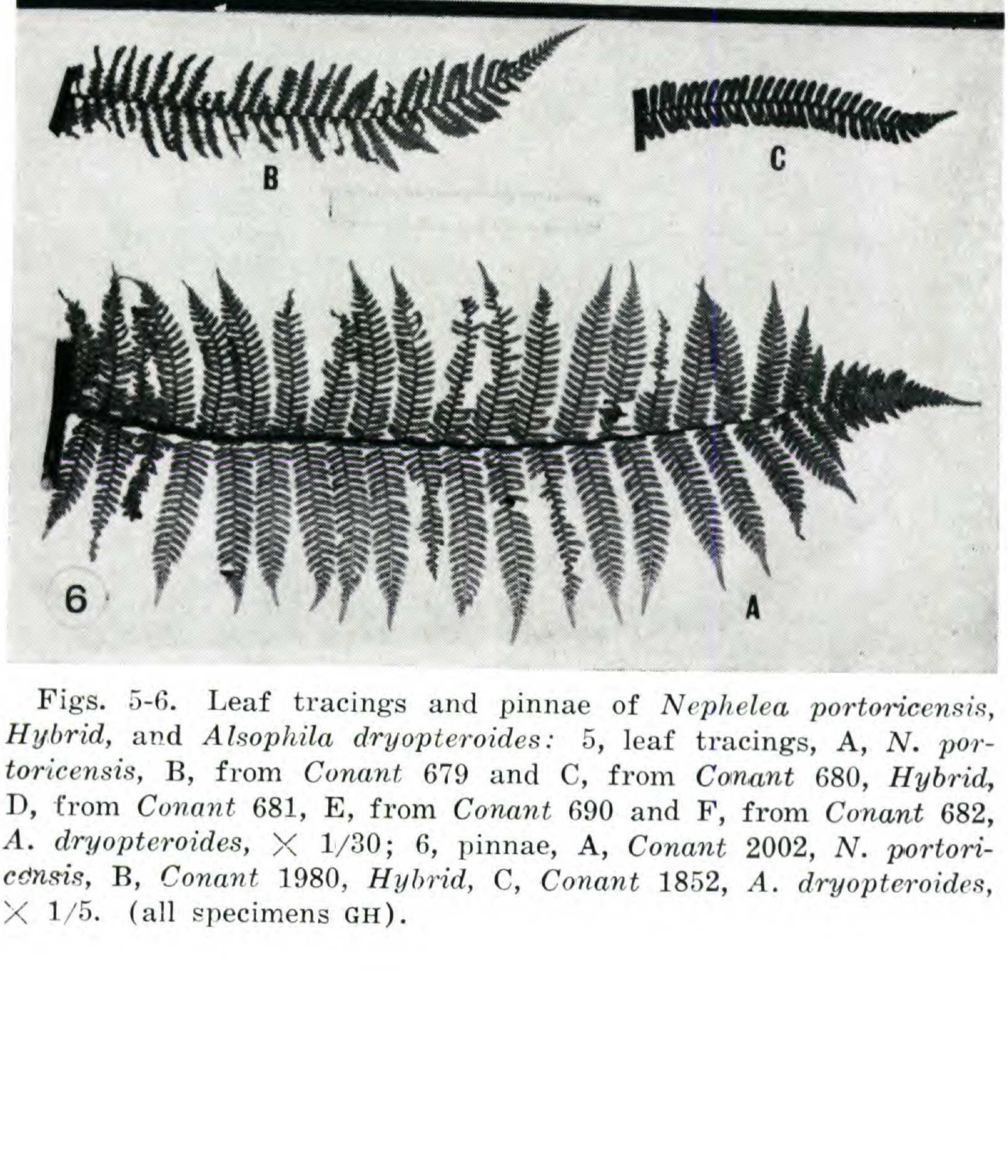
The black squaminate spines on the petiole and rachis (Fig. 10) are a generic character of *Nephelea* (Fig. 12). They firmly establish one parent as *N. portoricensis* since it is the only member of the genus in Puerto Rico. The setate scales on the lamina of the hybrid restrict the second parent to a species of *Alsophila* of which there are three in Puerto Rico; *A. Brooksii* (Maxon) Tryon, *A. bryophila*, and *A. dryopteroides*. *Alsophila Brooksii* is not known from the central mountains where the hybrids grew, it lacks the dark lanceolate type of scale present in the hybrid, and its long petiole is inconsistent with the requirements for the second parental species. Similarly, *A. bryophila* may be eliminated as a possible parent because it also lacks the dark lanceolate type of scale, and a parent with a short rather than a tall trunk is required. *Alsophila dryopteroides* remains as the second possible parent and all of the characters of the hybrid are consistent with this choice.

A detailed comparison of the hybrid and parental species is presented in Table 1. Some of the important characters of the hybrid are in the leaves, stems, and lamina scales.

Characters which are intermediate are lamina shape and dissection, stem, petiole and rachis spininess, number of leaf scars per unit of stem length, and leaf scar diameter. The lance-ovate lamina of the hybrid is intermediate be-

Figs. 1-2. *Alsophila dryopteroides* × *Nephelea portoricensis:* 1, plant, stem ca. 75 cm. tall, leaves ca. 1.0 m. long, *Conant* 679; 2, spore, × 1500, *Conant* 687. Figs. 3-4. *Cnemidaria horrida* × *Cyathea arborea:* 3, plant, stem ca. 2.0 m. tall, leaves ca. 2.5 m. long, *Conant* 626; 4, bicolorous scales on crozier, × 1/3, *Conant* 546. (all specimens GH).





Figs. 5-6. Leaf tracings and pinnae of *Nephelea portoricensis*, *Hybrid*, and *Alsophila dryopteroides:* 5, leaf tracings, A, *N. portoricensis*, B, from *Conant* 679 and C, from *Conant* 680, *Hybrid*, D, from *Conant* 681, E, from *Conant* 690 and F, from *Conant* 682, *A. dryopteroides*, × 1/30; 6, pinnae, A, *Conant* 2002, *N. portoricensis*, B, *Conant* 1980, *Hybrid*, C, *Conant* 1852, *A. dryopteroides*, × 1/5. (all specimens GH).

tween the oblanceolate lamina of *A. dryopteroides* and the ovate lamina of *N. portoricensis* (Fig. 5). The lamina dissection of the hybrid is bipinnate-lobed which is intermediate between the pinnate-pinnatifid condition of *A. dryopteroides* and the bipinnate-pinnatifid condition of *N. portoricensis* (Fig. 6). The stem, petiole and rachis of the hybrid have a few spines reaching 2.5 mm. long (Figs. 9 and 10), a condition which is intermediate between the spineless *A. dryopteroides* (Figs. 7 and 8) and the numerous spines reaching 5.5 mm. long in *N. portoricensis* (Figs. 11 and 12). The hybrid has from 18-25 leaf scars 1.5 cm. in diameter, per 10 cm. of stem (Fig. 9). *Alsophila dryopteroides* has about 43 leaf scars 1.0 cm. in diameter, per 10 cm. of stem (Fig. 7) while *N. portoricensis* has about 13 leaf scars 2.0 cm. in diameter, per 10 cm. of stem (Fig. 11).

One character of the hybrid is similar to that of *Alsophila dryopteroides*. The dark lanceolate laminar scales with a single apical seta found in the hybrid (Fig. 14) closely resemble the most prominent laminar scale of *A. dryopteroides* (Fig. 13).

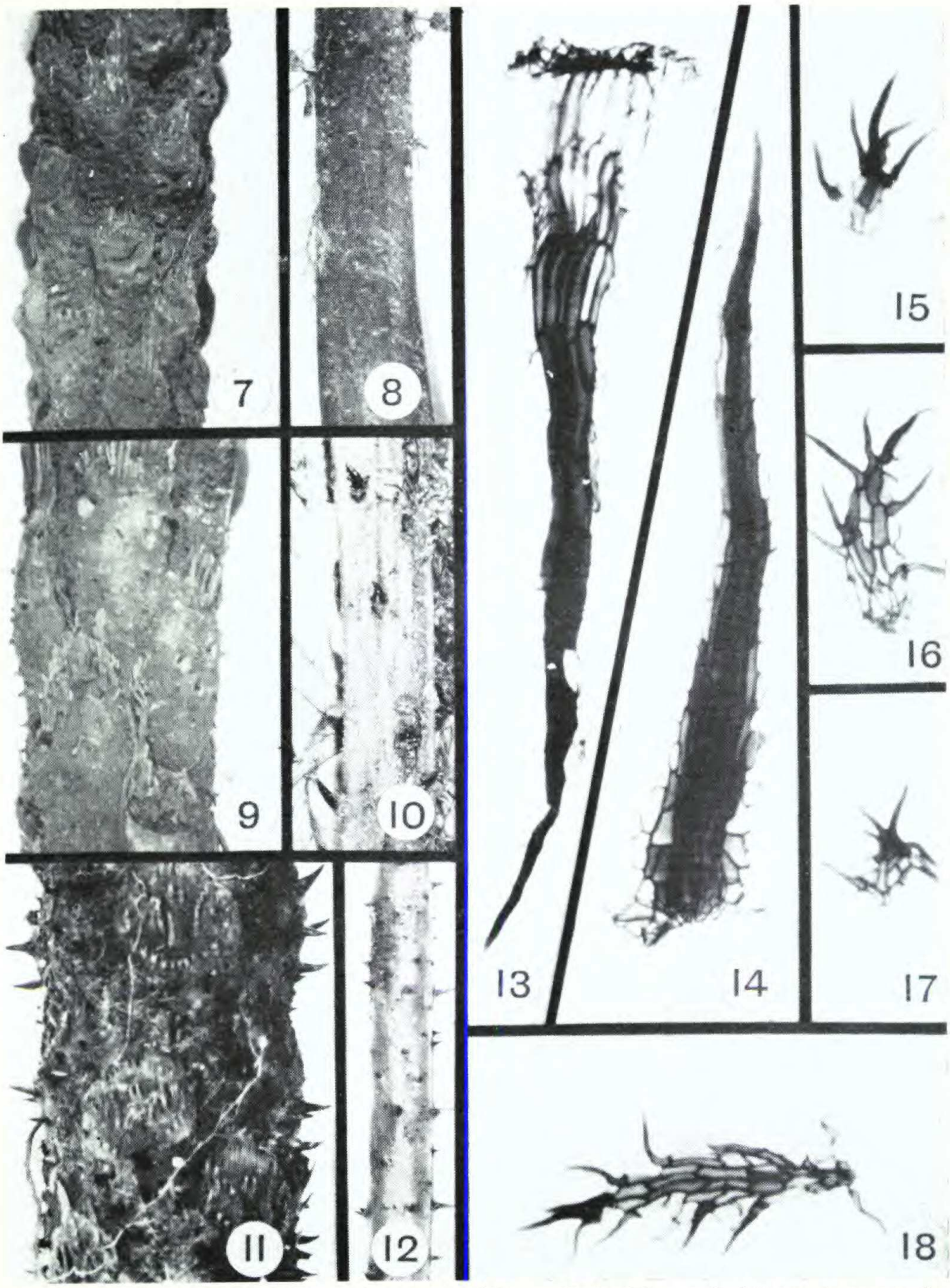
Other characters of the hybrid are like those of *Nephelea portoricensis*. The acaroid type of laminar scale occurs in both the hybrid (Fig. 15) and in *N. portoricensis* (Fig. 17) and the marginally setate type of scale also occurs in the hybrid (Fig. 16) and in *N. portoricensis* (Fig. 18).

The spores of the hybrid plants are well developed (Fig 2). A study of their viability has been planned but until it is completed it is not possible to suggest the number of F_1 hybrids probably involved in the five plants seen.

Trunk erect, occasionally short spiny, to 2 m. high, leaf scars 1.5 cm. in diameter, 18-25 per 10 cm. of stem length. Leaves 1.0-1.5 m. long, petiole to 10 cm., armed with short black squaminate spines; lamina lance-ovate, gradually narrowed at base (basal pinnae to ¼ as long as the median), to 60 cm. broad at the middle, acuminate, bipinnate-lobed to occasionally bipinnate-pinnatifid, leaf tissue glabrous,

Table 1. Character comparison of *Alsophila dryopteroides*, *Nephelea portoricensis*, and their hybrid.

Alsophila dryopteroides	Hybrid	*Nephelea portoricensis*
stem to 0.5 m., spineless	stem to 2.0 m., occasionally with short spines	stem to 4.0 m., with many long spines
leaf scar number ca. 43 per 10 cm. of stem length	leaf scar number 18-25 per 10 cm. of stem length	leaf scar number ca. 13 per 10 cm. of stem length
leaf scars 1.0 cm. in diameter	leaf scars 1.5 cm. in diameter	leaf scars 2.0 cm. in diameter
leaves to 1.0 m. long	leaves to 1.5 m. long	leaves to 2.0 m. long
petiole spineless	petiole with short squaminate spines, especially on the persistent base	petiole with long squaminate spines throughout
lamina oblanceolate	lamina lance-ovate	lamina ovate
pinna number to 40	pinna number to 25	pinna number to 13
basal pinnae reduced to auricles	basal pinnae ¼ the length of median ones	basal pinnae only slightly shorter than median ones
pinna-rachis undersurface without trichomes	pinna-rachis undersurface with a few trichomes	pinna-rachis undersurface with many trichomes
dark lanceolate laminar scales with single apical seta present	dark lanceolate laminar scales with single apical seta absent	dark lanceolate laminar scales with single apical seta absent
acaroid laminar scales absent	acaroid laminar scales present	acaroid laminar scales present
marginally setate laminar scales absent	marginally setate laminar scales present	marginally setate laminar scales present



Figs. 7-18. *Alsophila dryopteroides*, *Hybrid*, and *Nephelea portoricensis*. Figs. 7-8. *A. dryopteroides:* 7, stem, × 2/3, *Conant* 682, 8, petiole, × 2, *Conant* 690. Figs. 9-10. *Hybrid:* 9, stem, × 2/3, *Conant* 680, 10, rachis, × 2, *Conant* 680. Figs. 11-12. *N. portoricensis:* 11, stem, × 2/3, *Tryon & Tryon* 6950, 12, petiole, × 2/3, *Conant* 412. Fig. 13. *A. dryopteroides*, lanceolate type scale, × 100, *Conant* 598. Figs. 14-16. *Hybrid:* 14, lanceolate type scale, × 100, *Conant* 687, 15, acaroid scale, × 100, *Conant* 687, 16, marginally setate scale, × 100, *Conant* 687. Figs. 17-18. *N. portoricensis:* 17, acaroid scale, × 100, *Conant* 188, 18, marginally setate scale, × 100, *Conant* 188. (all specimens GH).

herbaceous, glaucescent beneath, dark green above; rachis dull castaneous, occasionally with short spines at the base, glabrescent to squamulose beneath, invested with stiff, brown, antrorse trichomes and a few long filiform scales above; pinnae to 25, spreading, sessile, the largest 30 cm. long, 7 cm. broad near base, becoming pinnatifid towards the apex; pinna-rachis beneath invested with marginally setate scales, acaroid scales, and dark bodied, light margined, lanceolate scales with a single, dark, stout apical seta, and with intermediate scales ranging from oblong to lanceolate, uniformly brown to dark bodied, and many setate to singly and stoutly setate, these latter types becoming sub-bullate towards the apex; undersurface of pinna-rachis becoming sparsely pubescent apically; pinnules 18-24 pairs, 19-34 mm. long, 7-10 mm. broad, deeply lobed to occasionally pinnatifid at the base; costa beneath often with acaroid scales at the base, and beyond with sub-bullate scales with few to many setae, these progressing to bullate scales at the pinnule apex, occasionally with a few stiff trichomes apically; costules with marginally setate sub-bullate scales at the base, these grading into squamules apically; veins 4-5 pairs, sori 2-3 on each lobe, closer to the costule than to the margin; indusia deeply cyathiform, tan, membranous, glabrous; spores well developed, light tan, trilete.

SPECIMENS EXAMINED:

Puerto Rico: Five plants from the vicinity of Cerro de Punta, 40 miles w.s.w. of San Juan, ravine on north side of road, Rt. 143, km. 18.5 e. of jct. with Rt. 10, *Conant* 678 (GH, NY, US), *Conant* 679 (GH, NY, US), *Conant* 680 (GH, NY, US), *Conant* 687 (F, GH, IJ, NY, RPPR, US, USD, Herb. El Verde Field Station, Puerto Rico); ravine on north side of road, Rt. 143, km. 22.2 e. of jct. with Rt. 10, *Conant* 599 (GH).

2. **Cnemidaria horrida** (L.) Presl × **Cyathea arborea** (L.) Sm. *Hemitelia Wilsonii* Hook. in Hook. & Baker, Syn. Fil. 30. 1865. TYPE: Jamaica, *Wilson* 731 (K). (See Maxon, Contrib. U.S. Nat. Herb. **17:** *t. 18.* 1914.)

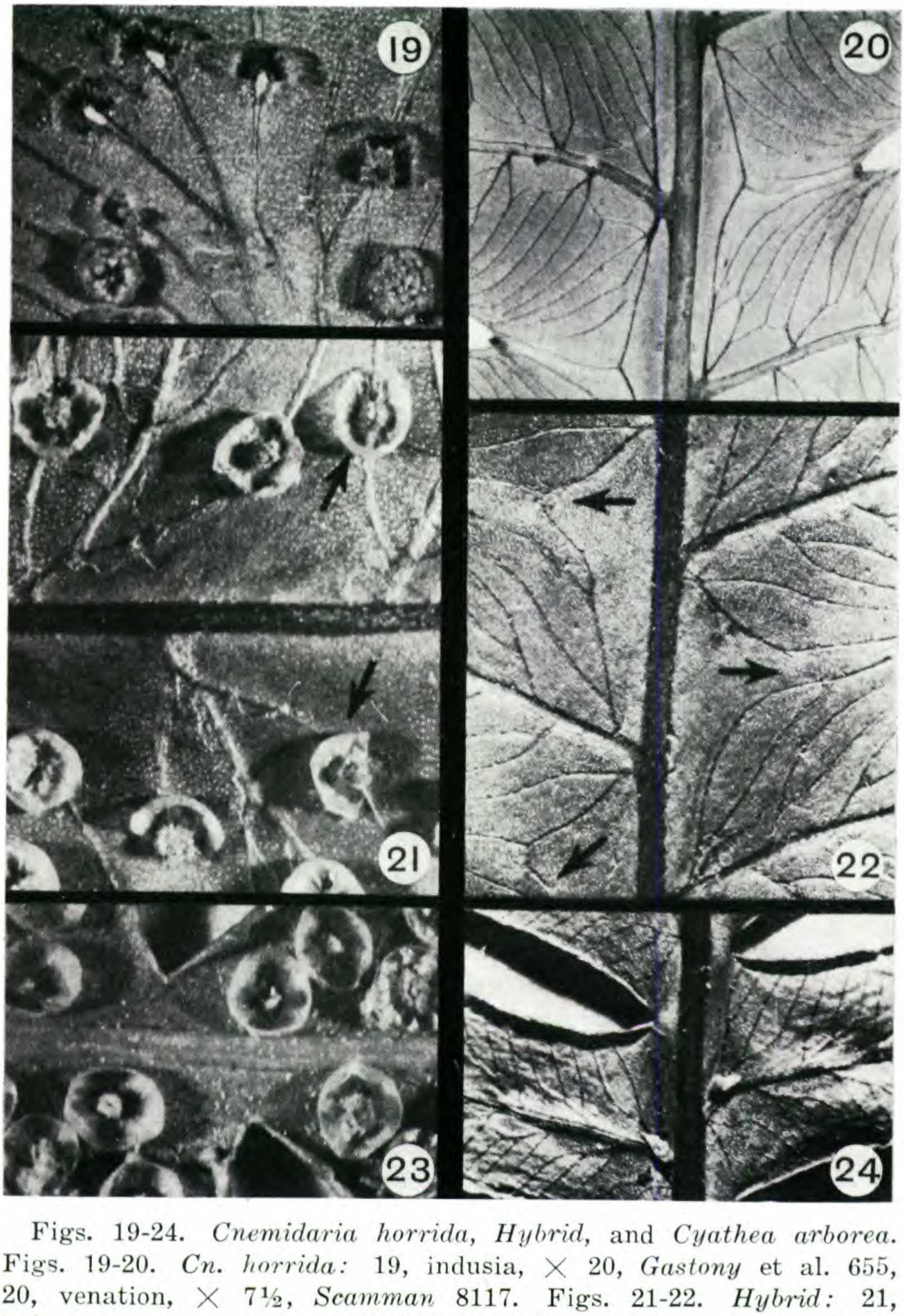
The status of *Hemitelia Wilsonii* (Fig. 3) as a species is untenable because well developed spores have not been found in its sporangia. Other factors indicating a hybrid status are the highly variable leaf architecture and the variable venation.

I have seen *Hemitelia Wilsonii* growing at two sites in the Luquillo Forest, 20 miles e.s.e. of San Juan, Puerto Rico (Rt. 186, km. 19.0 s. of jct. with Rt. 3, Municipio de Rio Grande, and Sabana Rd., km. 3.0 e. of jct. with Rt. 191, Municipio de Rio Grande). In both places *Cnemidaria horrida* and *Cyathea arborea* were growing nearby.

The hybrid is intermediate between the parental species in its venation, indusia, and leaf architecture. The venation of the hybrid is usually free but occasionally anastomoses or forms loops or dead-ends or both (Fig. 22). This condition is intermediate between the free venation of *Cyathea arborea* (Fig. 24) and the anastomosing venation of *Cnemidaria horrida* (Fig. 20). The indusia of the hybrid range from hemiteloid to sub-cyathiform (Fig. 21), a condition intermediate between the hemiteloid indusia of *Cn. horrida* (Fig. 19) and the cyathiform indusia of *C. arborea* (Fig. 23). The leaf architecture of the hybrid ranges from bipinnate-lobed to bipinnate-pinnatifid. This is intermediate between the pinnate-pinnatifid condition of *Cn. horrida* and the bipinnate-pinnatifid to tripinnate architecture of *C. arborea*.

Characters of the hybrid which are closest to *Cnemidaria horrida* are the shape of the pinna and leaf apex and the bicolorous scales on the croziers and petioles (Fig. 4). One character of the hybrid which is found in *Cyathea arborea* but not in *Cn. horrida* is the small whitish scales on the costa undersurface.

The apparent absence of viable spores, the combination of characters, and the documented occurrence of *Hemitelia Wilsonii* in the vicinity of both parental species, support the proposal of *H. Wilsonii* as a hybrid between *Cnemidaria horrida* and *Cyathea arborea*.



Figs. 19-24. *Cnemidaria horrida*, *Hybrid*, and *Cyathea arborea*. Figs. 19-20. *Cn. horrida:* 19, indusia, × 20, *Gastony* et al. 655, 20, venation, × 7½, *Scamman* 8117. Figs. 21-22. *Hybrid:* 21, indusia, upper arrow, subcyathiform indusium, lower arrow, hemiteloid indusium, × 20, *Gastony* et al. 654, 22, venation, upper arrow, anastomosing veins, middle arrow, space between free veins (note loop in lower vein), lower arrow, dead-end in vein, × 7½, *Conant* 546. Figs. 23-24. *C. arborea:* 23, indusia, × 20, *Howard & Nevling* 15776, 24, venation, × 7½, *Gastony* 10. (all specimens GH).

SPECIMENS EXAMINED:

Puerto Rico: *Conant* 546, 626, 627 (GH), *Hess* 371 (NY), *Hioram* 182, 804 (NY), *Kepler*, Sabana Rd., El Yunque Rd., 5 Mar., 1970, Herb, El Verde Field Station, Municipio de Rio Grande. **Dominican Republic:** *Abbott* 2660 (GH, NY, US), *Ekman* 14752 (NY), 15014 (GH, NY), *Gastony, Jones & Norris* 654 (GH). **Haiti:** *Ekman* H4835 (NY, S), H4846 (S, US). **Jamaica:** *Jenman* (NY), *Proctor* 18419 (A).

PUTATIVE HYBRIDS

The establishment of the *Alsophila-Nephelea* intergeneric hybrid with a bipinnate-lobed leaf architecture helps to interpret other rare species and unusual collections with a similar architecture within the *Alsophila-Nephelea* evolutionary line. These are discussed below in order of the certainty of their parental species. All of them combine characters of species with very different leaf architecture and (or) lamina indument. All are very rare, known mostly from one collection, and do not fit within the variation of the species proposed as parents. *Nephelea cinna* may be a hybrid, perhaps between *N. pubescens* and *N. Tussacii* as suggested by Gastony (1973) but a detailed analysis of it has not been made.

3. **Alsophila Brooksii** (Maxon) Tryon × **Nephelea portoricensis** (Kuhn) Tryon

A collection from Indiera Fria, near Maricao, Puerto Rico (*Britton, Cowell, & Brown* 4520 (NY)) resembles the *Alsophila dryopteroides – Nephelea portoricensis* hybrid quite closely in leaf dissection and in width to length proportions of the pinnae and pinnules. It differs in that it lacks the dark bodied, light margined, lanceolate scales with a single, dark, stout apical seta of *A. dryopteroides*. In addition the lamina base is abruptly narrowed, and the petiole is up to 25 cm. long. The complexity of the lamina, the abundance of acaroid scales, and the pubescence of the veins and costules of this collection are all characters attributable to *N. portoricensis* as pointed out by Gastony (1973). The unusually long and narrow pinnae suggest that this may be a hybrid involving *N. portoricensis* and

an *Alsophila* species with a less dissected lamina and long narrow pinnae. *Alsophila Brooksii* is well known from the Maricao Forest about 10 km. to the west of Indiera Fria. It is the only species of *Alsophila* occurring in the western end of the island, and it has a pinnate-pinnatifid lamina abruptly reduced at the base. It has long narrow pinnae and its petiole reaches 78 cm. in length. Its characters, combined with those of *N. portoricensis*, would result in a plant very similar to the *Britton et al.* 4520.

4. **Nephelea balanocarpa** (D. C. Eaton) Tryon × **Nephelea woodwardioides** (Kaulf.) Gastony

Cuban material with bipinnate-lobed lamina architecture such as *Leon, Clement, & Roca* 10533 (NY) and *Hioram & Clement* 6377 (US) seems to represent hybrids between pinnate-pinnatifid and bipinnate-pinnatifid species. One parent is probably the bipinnate-pinnatifid *Nephelea woodwardioides*. It is not clear whether var. *woodwardioides* or var. *cubensis* (Maxon) Gastony is involved. *Nephelea balanocarpa* is probably the second, pinnate-pinnatifid parent. It is far more common than *A. Brooksii*, also *pinnate-pinnatifid*, which is known in Cuba only from the type collection. The abundance of tiny antrorse squamules covering the veins in the hybrid is in agreement with the indument of *N. balanocarpa*.

5. **Alsophila hotteana** (C.Chr. & Ekman) Tryon × **Nephelea sp.** *Cyathea confinis* C. Chr. Kungl. Svensk. Vetens.-akad. Hand. ser. 3, **16**:13. 1937. TYPE: Haiti, Massif de la Hotte, Jeremie, *Ekman* 10382 (holotype, S; isotype, US!).

Cyathea confinis, a Haitian species known only from the type collection at Massif de la Hotte, has a bipinnate-lobed lamina, suggesting that it is probably of hybrid origin. It is described as having an aculeate trunk to 2 m. high, a short petiole armed with short black spines, and a gradually reduced lamina base. A relationship to the genus

Nephelea is evident in the aculeate trunk and the black petiole spines. Three species of the genus occur in Haiti, *N. crassa* (Maxon) Tryon, *N. fulgens* (C.Chr.) Gastony, and *N. woodwardioides* (Kaulf.) Gastony var. *Hieronymi* (Brause) Gastony. All are tall and have a bipinnate-pinnatifid lamina making it difficult or impossible to determine from herbarium specimens which of the species is involved in the cross.

Alsophila hotteana is probably the pinnate-pinnatifid parent. Its short petiole, gradually narrowed lamina base, and tall stem are consistent with the characters required of the second parent, and it is the only *Alsophila* known to occur in the Massif de la Hotte. Other species of *Alsophila* in Haiti are restricted to the Massif du Nord.

Putative Hybrids Involving Undetermined Species of Alsophila and Nephelea

6. *Cyathea irregularis* Brause Urban Symb. Ant. 7. 155. 1911. TYPE: Dominican Republic, Santo Domingo, Constanza, *Turckheim* 3212 (holotype, B; isotype, NY!).

Cyathea irregularis, known only from the type collection, is another species with a bipinnate-lobed lamina. It is evidently a hybrid of *Alsophila* and *Nephelea* since all species of *Alsophila* in the Dominican Republic are pinnate-pinnatifid and all species of *Nephelea* are bipinnate-pinnatifid. The single specimen of a midportion of the lamina, however, provides too few characters to choose between the four Alsophilas and three Nepheleas known to grow in the country.

Another specimen from the Dominican Republic, with a similar leaf morphology, *Abbott* 2031 (US, pro parte) is probably an *Alsophila* × *Nephelea* hybrid but may not have the same parents as *Cyathea irregularis*.

7. *Cyathea jamaicensis* Jenm. Jour. Bot. **20**: 323. 1882. TYPE: Jamaica, Mansfield, near Bath, *Wilson* 686 (holotype, BM; isotype, GH!).

The bipinnate-lobed *Cyathea jamaicensis* is known only from the type collection. It is similar to *Nephelea concinna*, but may be separated from it by its pinna rachis indument and by its indusium. *Cyathea jamaicensis* has the undersurfaces of its pinna-rachises nearly without scales and trichomes and it has a meniscoid indusium. *Nephelea concinna* has its pinna-rachis undersurfaces quite well invested with scales and trichomes and it has a cyathiform to urceolate indusium. Also, *C. jamaicensis* is described as having an unarmed stem whereas *N. concinna* has a spiny stem.

It seems probable that *Cyathea jamaicensis* is a hybrid because of its lamina architecture and its rarity. The lack of spines on its trunk implies that it could not be an intrageneric cross involving two species of *Nephelea*. The degree of lamina dissection of *C. jamaicensis* suggests that a bipinnate-pinnatifid species of *Nephelea* has crossed with a pinnate-pinnatifid species of *Alsophila*.

CONCLUSIONS

Two certain and five putative hybrids have been proposed. All combine characters of species with very different leaf architecture, lamina indument, and (or) indusia. The implication is that other species with similar leaf architecture, lamina indument, and (or) indusia should also cross. These hybrids would be very difficult or impossible to detect. Some polymorphic species in current taxonomic treatments may require reassessment because hybrids may have been included in the taxa. Careful field observations of species that are growing together, whenever tree fern collections are made, will help to solve this problem.

The presence of well developed spores in the *Alsophila dryopteroides* × *Nephelea portoricensis* hybrid suggests that these genera are closely related. The apparent absence of well developed spores in the *Cnemidaria horrida* × *Cyathea arborea* hybrid implies a more distant relation of the parents.

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